

SALAMANDERS OF THE NORTHWESTERN HIGHLANDS OF GUATEMALA

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ABSTRACT. The salamander faunas of the Cordillera de los Cuchumatanes and the Montañas de Cuilco of western Guatemala are reviewed in light of extensive new collections. Thirteen species are reported from the Cuchumatanes including one new member of the *Bolitoglossa mexicana* species group, herein described as *Bolitoglossa jacksoni* sp. nov., and four recognized species never before collected in the massif (*Bolitoglossa hartwegi*, *B. mulleri*, *B. rufescens* and *Dendrotriton rabbi*). Four species are reported from the Cuilco including two hitherto unknown from that mountain range (*Bolitoglossa morio* and *Pseudoeurycea rex*).

Bolitoglossa resplendens (sensu lato) lacks the features purported to differentiate it from *B. lincolni* and is considered a junior synonym. Based on gross morphological similarity, the *Bolitoglossa helmrichi* and *B. rostrata* species groups are divided and reconstituted into four species groups (*dunni*, *franklini*, *morio* and *veracruis* groups).

The Cuchumatanes support fewer salamander species but a larger number of species groups and genera than do the Pacific Uplands. The diversity differences are correlated with greater age and connectedness among high elevation salamander habitats in the Cuchumatanes relative to the Pacific Uplands.

Salamander species on the Cuchumatanes and Cuilco occur in narrow elevational belts as they do on the Pacific Uplands. Conspecific populations or related species tend to occur at comparable elevations wherever found. Within-group variation in elevational range does exist, however, and much of it is correlated with geographic variation in the elevation of the cloud line. The *Bolitoglossa veracruis* species group is exceptional among Nuclear Central American salamander groups in the extreme breadth of the combined elevational ranges of its three member species (2,800 m; the next broadest is 1,200 m). The great ecological scope of the *Bolitoglossa veracruis* group may have been a crucial factor in the invasion of the lowlands by *Bolitoglossa* beta.

RESUMEN. Las faunas de salamandras de la Cordillera de los Cuchumatanes y de las Montañas de Cuilco en el oeste de Guatemala se revisan en base a las extensas nuevas colecciones realizadas. Trece especies se encuentran en los Cuchumatanes, incluyendo una nueva especie, *Bolitoglossa jacksoni*, miembro del grupo específico de *Bolitoglossa mexicana*, y cuatro especies ya descritas pero nunca encontradas en esta sierra previamente (*Bolitoglossa hartwegi*, *B.*

mulleri, *B. rufescens* y *Dendrotriton rabbi*). Cuatro especies se encuentran en el Cuilco incluyendo dos anteriormente desconocidas en esta región (*Bolitoglossa morio* y *Pseudoeurycea rex*).

Bolitoglossa resplendens (sensu lato) no tiene las características que supuestamente la diferencian de la *B. lincolni*, y consecuentemente *B. resplendens* es un sinónimo. En base de similitudes en morfología externa, los grupos específicos de *Bolitoglossa helmrichi* y *B. rostrata* descritos por Wake y Lynch (1976) son divididos y redefinidos en cuatro grupos (*dunni*, *franklini*, *morio* y *veracruis*).

En los Cuchumatanes habitan menos especies de salamandras pero un número mayor de grupos específicos y géneros, en comparación con las montañas del lado Pacífico. Estas diferencias de diversidad están correlacionadas con una edad geológica mayor y con una mayor conexión entre regiones de alta elevación en comparación con las montañas del lado Pacífico.

Las especies de urodelos en los Cuchumatanes y el Cuilco se localizan en estrechas bandas elevacionales al igual que en las montañas del Pacífico. Poblaciones de la misma especie, o especies relacionadas, generalmente se encuentran en la misma zona elevacional. Pero, si se encuentra variación al nivel de intra-grupo, la mayor parte de esta variación está correlacionada con la variación geográfica a la altura de la zona nublada. El grupo específico de *Bolitoglossa veracruis* es una excepción entre todos los grupos de Centro America Nuclear debido a la extrema distribución elevacional de las tres especies miembros (2,800 m); la segunda distribución mas amplia es 1,200 m. El gran alcance geológico de este grupo puede tener un papel importante en la historia de la invasión de las tierras bajas por *Bolitoglossa* beta.

INTRODUCTION

Nuclear Central America (NCA), the landmass bounded to the northwest by the Isthmus of Tehuantepec and to the southeast by the Nicaraguan depression, contains six major highland masses isolated from one another by deep dry valleys (Fig. 1). The Cordillera de los Cuchumatanes and the Montañas de Cuilco are two limestone capped ranges, respectively about 3,000 and 400 square kilometers in extent and 4,000 and 3,400 meters at greatest elevation (Fig. 2).

On the Caribbean slope of the Cuchumatanes, tropical rain forest (following the ecological terminology of Schmidt, 1936) extends from near sea level to a 1,300 m "cloud line" (that characteristic elevation at which the water carried by rising

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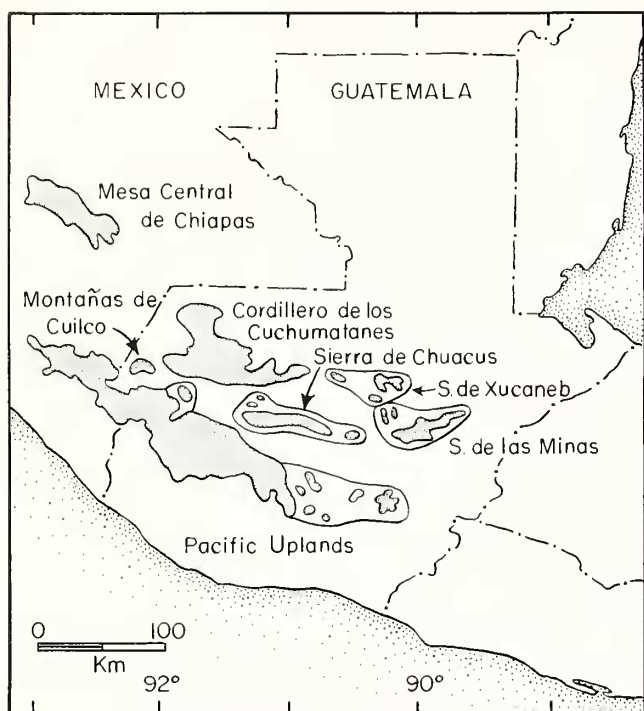


Figure 1. Nuclear Central America. The 2,100-m contour interval is stippled.

humid air condenses in the form of fog). Above the cloud line is a zone of extremely wet broadleaf and treefern forest, the subtropical zone cloud forest, which grades upward into drier but still humid subtropical forest that is frequently composed of oak. At about 2,700 m, varying locally, the pine and cypress temperate zone forests commence, continuing to the 3,400-m treeline, above which bunchgrass predominates.

The above vegetational series is found on the unobstructed face of the Caribbean slope; but, in the protected interior valleys, variably drier systems occur, typically dominated by pine-oak forest even at low elevation. Because of their protected position, the Montañas de Cuilco have an abbreviated form of the ecological pattern found on the open escarpment: as in the Cuchumatanes, pine and cypress dominate down to about 2,700 m, where a wet broadleaf forest begins; however, a high cloud line occurs at about 2,000 m, and dry scrubby pine-oak growth predominates below this level.

The salamander faunas of the Cordillera de los Cuchumatanes and the Montañas de Cuilco of western Guatemala have been little sampled or reported upon. In the Cuchumatanes Stuart (1943a, 1943b) made the first collections and reported four species referred to *Oedipus*: *lincolni*, *cuchumatani*, *rostratus*, and *rex*. From later collections Stuart (1952) described *Magnadigita omniumsanctorum*. The next discovery in the Cuchumatanes was recorded by Lynch and



Figure 2. Montañas de Cuilco and the Cordillera de los Cuchumatanes with the 2,100-m contour interval and regional landmarks.

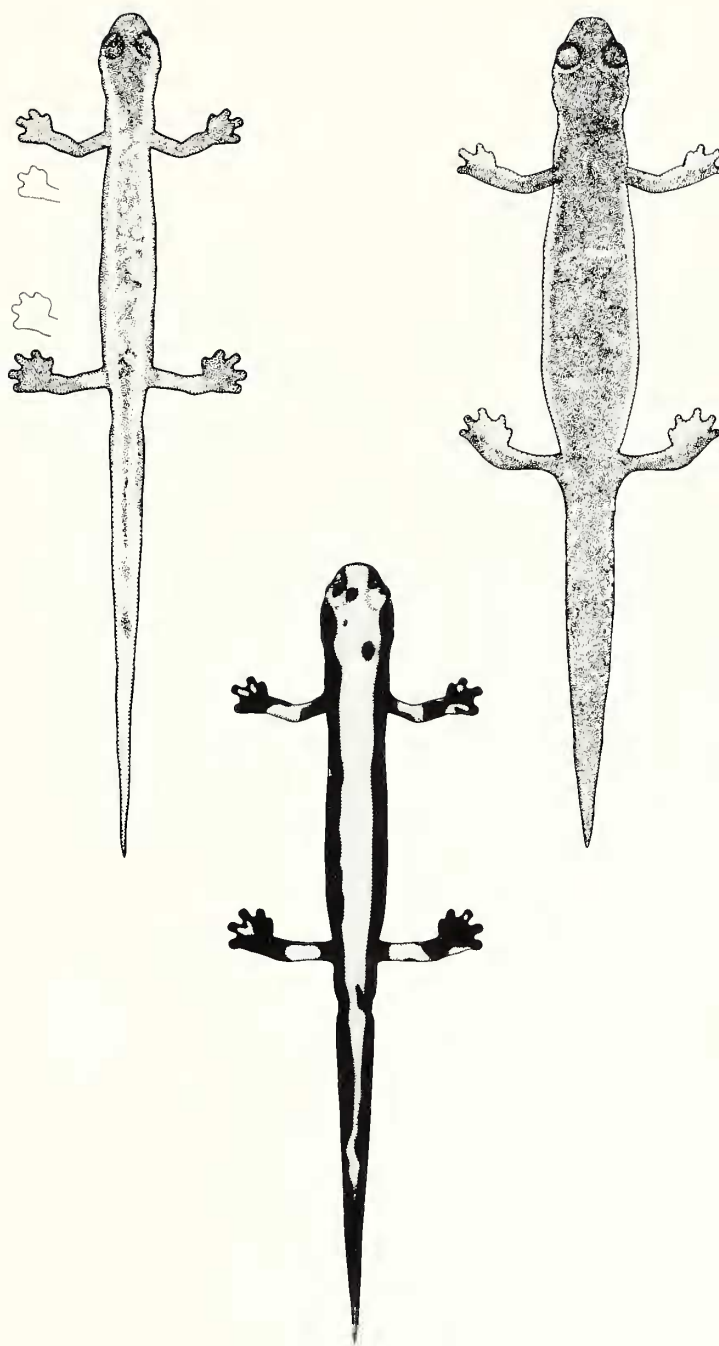


Figure 3. *Bolitoglossa rostrata*, *B. cuchumatana*, *B. morio*, and *B. lincolni*, life size. UPPER LEFT: *Bolitoglossa rostrata*, body, legs, and flanks dark brown, bilateral shoulder stripes lighter brown with middorsal brown mottling. A unicolor brown morph also is found. UPPER LEFT INSET: Feet of *B. cuchumatana*. Overall coloration like that of *B. rostrata*. UPPER RIGHT: *B. morio*, dark slate grey all over except for light speckling on flanks and anterior surfaces of limbs, and light lateral spotting on tail (Cuilco specimen figured; Cuchumatán specimens have light spotting on flanks as well as tail). BOTTOM CENTER: *B. lincolni*, black ground color with a coral red dorsal swath and spotting on limbs and (occasionally) venter. In some specimens, the dorsal swath is reduced to a series of red spots.

Wake (1975) with the naming of *Chiropterotriton cuchumatanus*. Finally, Elias and Wake (1983) and Wake and Elias (1983) named two new monotypic genera, *Nyctanolis pernix* and *Bradytriton silus*, both from the cordillera.

Prior to the present study the only salamanders that had

been collected in the Montañas de Cuilco were *Bolitoglossa resplendens* (*sensu lato*) and *Chiropterotriton rabbi*, both first reported by Lynch and Wake (1975).

Bolitoglossa stuarti was described from the valley separating the Cuilco from the Cuchumatanes (Wake and Brame,

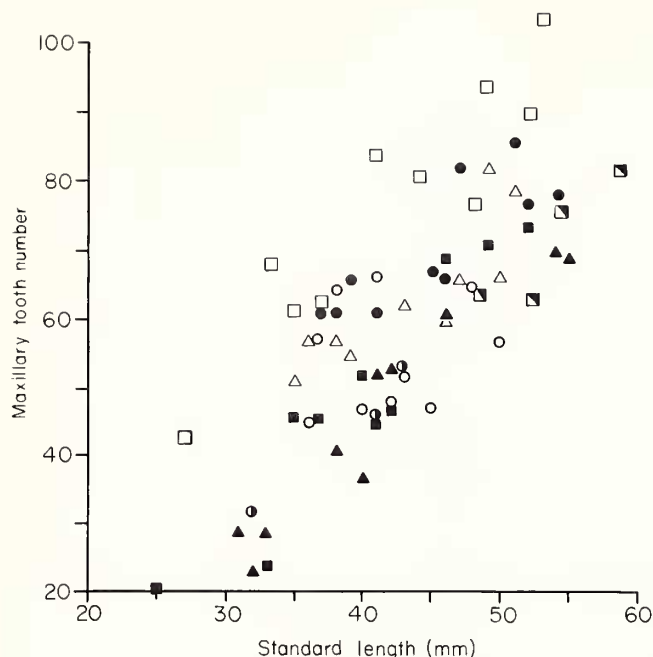


Figure 4. Relationship between maxillary tooth number (both sides summed) and standard length in the *Bolitoglossa dunni* complex. Solid triangle = *B. cuchumatana* (Eastern Cuchumatanes); open triangle = *B. cuchumatana* (Western Cuchumatanes); half-filled circle = *B. helmrichi* (Chuacús); solid circle = *B. helmrichi* (Western Minas); open circle = *B. helmrichi* (Xucaneb); solid square = *B. engelhardti* (Pacific Uplands); open square = *B. sp.* (Eastern Cuchumatanes); half-filled square = *B. dunni* (Honduras).

1969) and is the only salamander species known from the valley. As a low elevation form this species will be mentioned only in the discussion.

In the course of the present study twelve salamander species were documented for the Cuchumatanes, bringing the total number of known forms from six to thirteen for the mountain range. Among the seven species previously unknown from the massif were the two new monotypic genera described elsewhere (Elias and Wake, 1983; Wake and Elias, 1983) and the one new member of the *Bolitoglossa mexicana* species group described below. Four species were taken in the Montañas de Cuilco during this work. All of these were recognized forms, but two were previously unknown from those mountains.

This paper provides a species account for each of the salamander species now known from the Cuchumatanes and Cuilco, including taxonomic synonymies, type locality, geographic range, habits and habitat preferences and a discussion of the geographic variation and possible evolutionary relationships of the taxon. The discussion section is divided into three parts. In the first part, the species groups within *Bolitoglossa* beta (*sensu* Wake and Lynch, 1976) are redefined. In the second part, contemporary patterns of distribution and differentiation are examined to provide insight into the history of the salamander fauna. In the third part, patterns of elevational distribution are presented for the Cuchuma-

tanés and Cuilco and are discussed relative to the results of Wake and Lynch (1976) for the Pacific Uplands.

SPECIES ACCOUNTS

Bolitoglossa cuchumatana (Stuart, 1943)

Figure 3

Oedipus cuchumatanus Stuart, 1943a:14.

Magnadigita cuchumatana: Taylor, 1944:218.

Bolitoglossa cuchumatana: Wake and Brame, 1963:386.

TYPE LOCALITY. Oak woods 2 km N Nebaj, Depto. Quiché, Guatemala, 1,900 m elevation.

RANGE. Stuart collected this form only at the type locality. Wake, Houck, and Lynch next found the species 25 years later about 15 km to the south and 600 m higher in elevation. I found *B. cuchumatana* at two additional sites in the western Cuchumatanes near Chiapas and at the easternmost end of the range, near San Miguel Uspantán.

HABITAT AND HABITS. *B. cuchumatana* have been taken on the ground, under bark, and in arboreal bromeliads where they have been found active on surface debris on wet evenings from the 1,200-m cloud line through the subtropical cloud forest to 2,500 m.

SYSTEMATICS. A series of species, including *Bolitoglossa engelhardti* in the Pacific Uplands, *B. helmrichi* in the Xucaneb and Western Minas, a newly discovered population (possibly representing a new species) in the Eastern Minas, *B. cuchumatana* in the Cuchumatanes, and *B. dunni* in Hon-

Table 1. Geographic variation in subcaudal coloration and degree of interdigital webbing among the species of the *Bolitoglossa dunni* complex.

Species and population	Subcaudal coloration	Degree of interdigital webbing
<i>B. helmrichi</i> (Chuacús)	no data	high
<i>B. helmrichi</i> (Xucaneb)	orange	high
<i>B. helmrichi</i> (Western Minas)	orange	high
<i>B. sp.</i> (Eastern Minas)	tan	low
<i>B. cuchumatana</i> (Western Cuchumatanes)	tan	medium
<i>B. cuchumatana</i> (Eastern Cuchumatanes)	tan	medium
<i>B. engelhardti</i> (Pacific Uplands)	tan	medium
<i>B. dunni</i> (Honduras)	no data	medium

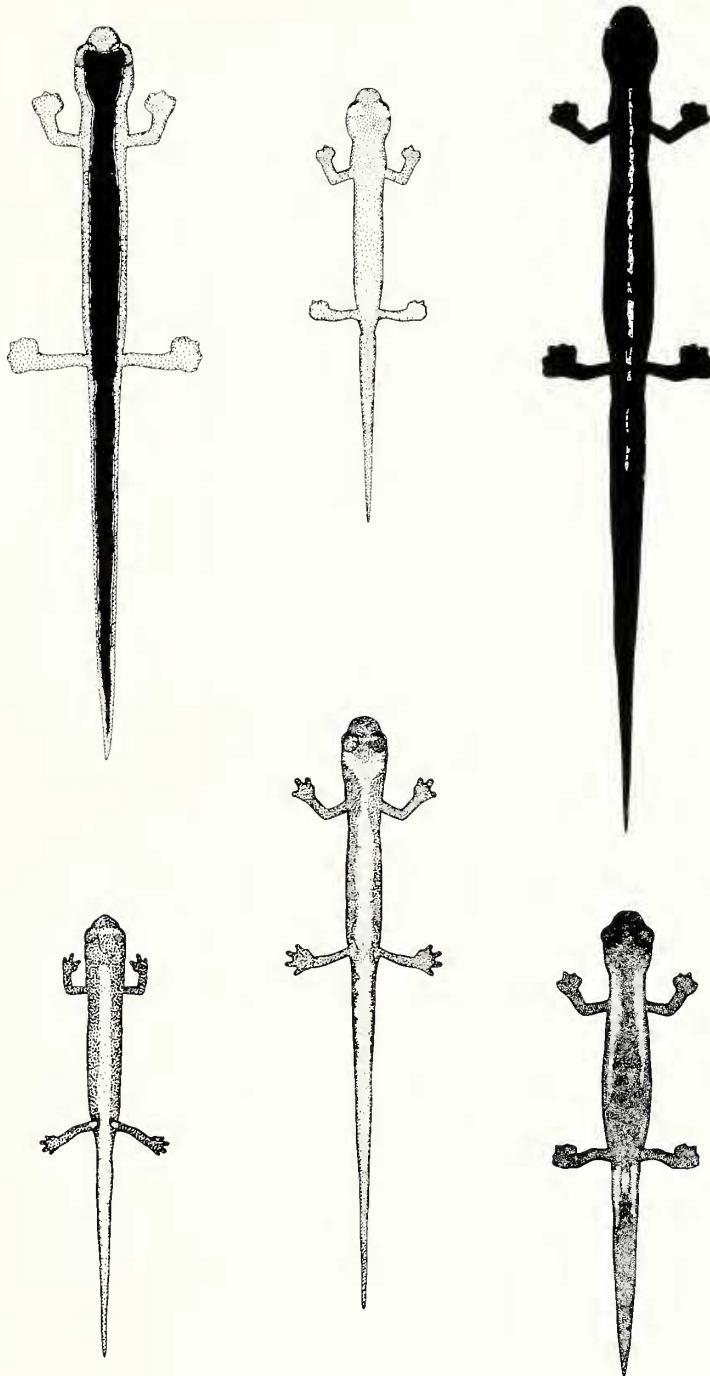


Figure 5. *Bolitoglossa jacksoni*, *B. rufescens*, *B. mulleri*, *Dendrotriton rabbi*, *D. cuchumatanus*, and *Bolitoglossa hartwegi*, life size. UPPER LEFT: *Bolitoglossa jacksoni* (holotype figured), background yolky yellow, middorsal swath dark brown with narrow white border. TOP CENTER: *B. rufescens*, tan overall with a slightly darker brown snout and flanks. Tone varies from light to dark brown both between individuals and for one individual at different times of day. UPPER RIGHT: *B. mulleri*, black overall except for a narrow broken vertebral stripe of tan. In some Cuchumatan specimens, the stripe is reduced or absent. LOWER LEFT: *Dendrotriton rabbi*, pattern composed of various shades of brown. Note light interorbital bar. Animals may have a reddish or even greenish cast. Pattern and tone variable between individuals. BOTTOM CENTER: *D. cuchumatanus*, similar to *D. rabbi* above. LOWER RIGHT: *Bolitoglossa hartwegi*, dark brown overall with lighter paired shoulder and pelvic stripes. Animals may be without markings altogether or may have small light streaks on dorsum at random.



Figure 6. *Bolitoglossa jacksoni* sp. nov., an adult female (escaped) from the type locality.

duras, appears to form a relatively homogeneous assemblage of related congeners. The group, which I shall call the *dunni* complex, was first outlined by Stuart (1943a) and is characterized by a moderate degree of foot webbing; by well-developed subdigital pads and the associated hypertrophy of the terminal phalanges; by a generally brown dorsal color frequently differentiated into light shoulder stripes and darker flanks; and by a common microhabitat (see Wake and Lynch, 1976, for information on the ecology of *B. engelhardti*).

The species in this series are most similar to *Bolitoglossa rostrata*, but differences in foot morphology (*B. rostrata* has little interdigital webbing) usually permit separation (see *B. rostrata* and compare inset *B. cuchumatana* feet, Fig. 3). *B. rostrata* occurs in limited sympatry with *B. cuchumatana* with no hybridization.

Despite the general similarities, variation between the species of the *B. dunni* complex is pronounced in the coloration of the subcaudal surface, the number of maxillary teeth, and the morphology of the foot. Data were collected for eight populations from the five *B. dunni* complex species (Fig. 4, Table 1). *B. helmrichi* can be defined on the basis of its high degree of interdigital webbing and orange subcaudal coloration to include populations in the Xucaneb, the Western Minas, and the Chuacús. *B. cuchumatana*, including all Cuchumatán specimens, and *B. engelhardti* are similar in their intermediate degree of interdigital webbing, tan subcaudal surface, and moderate tooth number, and are distinguishable from one another both on the basis of adult size

(*B. engelhardti* is smaller than any other member of the complex) and in frequency of shoulder striping (*B. engelhardti* is usually unmarked, while *B. cuchumatana* almost always has bilateral light striping). *Bolitoglossa dunni* occurs in both a pink and dark morph, the latter with light spotting (Schmidt, 1933), and it achieves larger size than any other member of the complex and has little webbing and low tooth numbers. The population from the Eastern Minas differs sharply from all other members of the *B. dunni* complex (and from all known *B. rostrata* populations as well) in having extremely high numbers of maxillary teeth. It has almost as little webbing as *B. rostrata*. That this population belongs in the *B. dunni* complex rather than to *B. rostrata* is suggested only by its occurrence at relatively low elevation.

Bolitoglossa hartwegi Wake and Brame, 1969

Figure 5

Bolitoglossa hartwegi Wake and Brame, 1969:10.

TYPE LOCALITY. 4.5 mi. W San Cristobal de Las Casas, Chiapas, Mexico. 7,000 ft elevation.

RANGE. *B. hartwegi* has been known only from the general vicinity of its type locality on the Mesa Central de Chiapas. It is here reported from Guatemala, both in the western Cuchumatanes at Finca Chiblac, and in the easternmost reaches of the range, near San Miguel Uspantán.

HABITAT AND HABITS. Specimens have been collected under bark on logs and stumps, under cover objects on the ground, in rock crevices, and in arboreal bromeliads; the

species is active on rainy nights. *B. hartwegi* have a broad elevational range, occurring from the 1,200-m cloud line to the lower temperate forest at over 2,700 m.

SYSTEMATICS. When these populations were discovered in the Cuchumatanes during this study they were assigned to the *Bolitoglossa veracrucis* species group (see Discussion) based upon their well-ossified skull with a broad pars dentalis of the premaxillary, and a derived foot morphology. They were assigned to the species *B. hartwegi* based on a mainly unicolor dorsum (*B. veracrucis* is streaked and mottled), a small size (*B. stuarti* is larger), and a mottled venter (unicolor in *B. stuarti*).

***Bolitoglossa jacksoni* new species**

Figures 5 and 6

HOLOTYPE. MVZ 134634, a young adult female from the Las Nubes sector of Finca Chiblac, approximately 12 km NNE of Santa Cruz Barillas, Depto. Huehuetenango, Guatemala, at about 1,400 m elevation, collected by Jeremy L. Jackson, 1 September 1975.

DIAGNOSIS. The new taxon is a large species of *Bolitoglossa* (the young adult holotype is 49.1 mm and another specimen was approximately 65 mm in standard length) with low numbers of maxillary teeth (31 in the holotype) and moderate numbers of vomerine teeth (21 in the holotype). The species is a member of the *Bolitoglossa* alpha group on the basis of its simple vertebral tail autotomy mechanism (Wake and Dresner, 1967; Wake and Lynch, 1976). It is distinguished from *B. salvinii*, *B. mexicana*, *B. mulleri*, *B. odonnelli*, *B. platydactyla*, and *B. flaviventris* in having dark coloration restricted to the middorsal region; separated from all other Nuclear Central American *Bolitoglossa* both by color pattern and its tail autotomy mechanism.

DESCRIPTION (OF HOLOTYPE). Nostril small; labial protuberances of nasolabial grooves small and poorly developed; canthus rostralis moderate in length, rounded and gently arched. Standard length 6.6 times head width; standard length 4.5 times snout-gular fold length (head length). Deep, unpigmented groove below eye extends almost full length of opening, following curvature of eye, but does not extend to lip. Eye moderate in size, slightly protuberant in life. Lightly indicated postorbital groove extends posterior and slightly ventrad as a shallow depression for 2.7 mm, thence proceeds directly ventrad and passes behind posterior end of mandible to produce a shallow but definite nuchal groove parallel to and 4.0 mm anterior to the clearly defined gular fold. The 21 vomerine teeth are arranged in single arched rows on either side of the midline and extend laterally to the level of the midpoint of the internal nares. The two rows of 31 maxillary teeth extend posteriorly to a level one-third of the way through the eye. Five small undifferentiated premaxillary teeth protrude from well behind the lip. The tail is round in cross section and is 0.8 times the standard length from base to tip; the postiliac gland is not evident. Limbs are of moderate length, three costal grooves are exposed between the toetips of the adpressed fore and hind limbs; standard length is 4.4 times right hind limb length

and 4.9 times right fore limb length. Standard length is 10.0 times the hind foot width and both fore and hind feet are fully webbed and lack subdigital pads; the toetips are rounded in dorsal aspect. The fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

MEASUREMENTS (OF HOLOTYPE). Head width (maximum), 7.4 mm; head length (snout to gular fold), 11.0 mm; head depth at posterior angle of jaw, 4.1 mm; eyelid length, 3.0 mm; eyelid width, 1.9 mm; anterior rim of orbit to snout, 2.6 mm; horizontal orbital diameter, 2.2 mm; interorbital distance, 3.0 mm; distance between vomerine teeth and parasphenoid tooth patch, 0.3 mm; snout to fore limb, 13.6 mm; distance separating internal nares, 2.2 mm; distance separating external nares, 2.1 mm; snout projection beyond mandible, 0.6 mm; snout to posterior angle of vent (standard length), 49.1 mm; snout to anterior angle of vent, 45.6 mm; axilla to groin, 27.4 mm; tail length, 43.4 mm; tail width at base, 3.7 mm; tail depth at base, 3.3 mm; fore limb length, 10.0 mm; hind limb length, 11.2 mm; width of hand, 3.7 mm; width of foot, 4.9 mm.

COLORATION IN ALCOHOL. The ground color is pale yellow with a broad middorsal swath of dark brown. The brown marking originates on the head at the level of the eyelids and extends in breadth from the center of one eyelid to the center of the other in a straight edge across the head. Posteriorly the brown stripe diminishes gradually until it disappears near the tail tip. Aside from the brown swath, the animal is unmarked (Fig. 5).

COLORATION IN LIFE. This animal was a brilliant yolky yellow. The dorsal swath was chocolate brown and was entirely bordered by an edging of immaculate white less than a millimeter in width. The eye was metallic gold (Fig. 6).

OSTEOLOGY. As the animal was preserved flat in standard pose, accurate measurements from a radiograph could be taken. Skull, from the anterior border of the premaxilla to the medial edge of the occipital condyles, 8.0 mm; width of pars dentalis of the premaxilla, 1.3 mm; maximum width of braincase (anterior to the otic capsules) 3.0 mm; maximum width of skull base (across otic capsules) 4.9 mm; longest axis of otic capsule, 2.6 mm; and straight line length of the maxilla from anterior to posterior tip, 4.5 mm.

The preorbital process of the vomer extends well lateral to the internal narial opening as a slender sliver that tapers to a point. The frontal processes of the premaxilla arise and continue well separated from one another, spreading gradually as they rise dorsad and posteriorly. Septomaxillae are absent. Trunk vertebrae number 14, caudosacral 2, and caudal 30. No tibial spur is evident; phalangeal formulae are 1, 2, 3, 3, 2 for the foot and 1, 2, 3, 2 for the hand. Phalanges are broadened and slightly irregular in outline, and the terminals of the three outer fingers and four outer toes are laterally expanded such that each is broader than it is long. The innermost toe and finger have terminals that are pointed and curved along the rim of the pad toward the other digits.

VARIATION. Two specimens of this form were collected, but one, a large adult female, escaped before it could be preserved. Knowledge of variation is thus restricted to aspects of color and pattern that were preserved in photographs

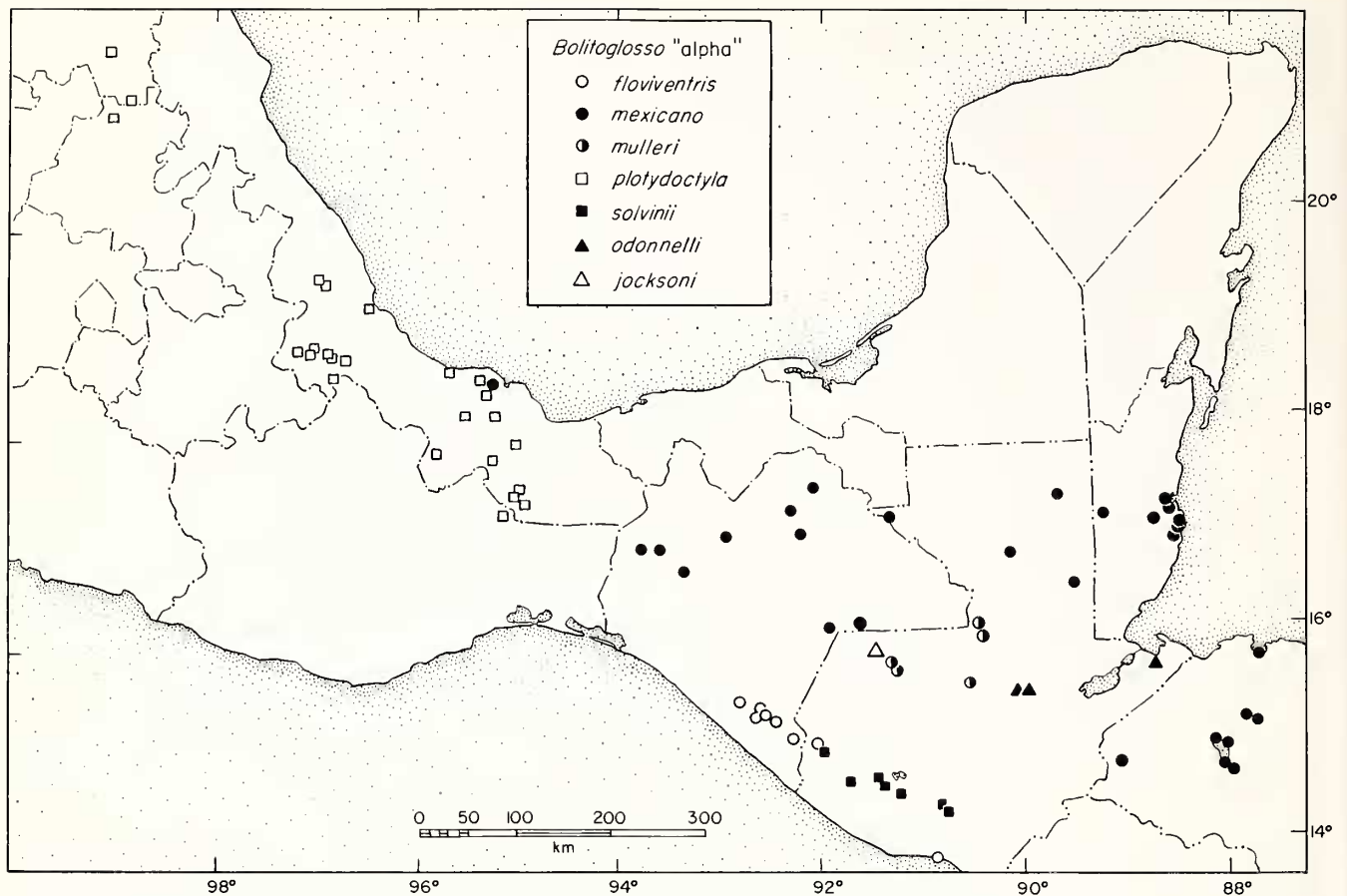


Figure 7. Distribution of the *Bolitoglossa mexicana* species group (modified from Wake and Lynch, 1976).

of the escaped animal (Fig. 6, and Hanken et al., 1980). All the hues described for the holotype were similar in the other individual, but the latter had a more irregular dorsal pattern. The brown dorsal swath was interrupted by a large yellow nape spot and a break on the tail, and the white border was incomplete. In addition a spot of brown was present on the dorsal surface of the right hind foot.

RANGE. *Bolitoglossa jacksoni* has been taken only within 1 km of the type locality on the Caribbean escarpment of the western Cuchumatanes (Fig. 7).

HABITAT AND HABITS. Both individuals were taken under bark of felled hardwood logs in clearings in a subtropical forest, which receives upward of 6 m of rain annually.

SYSTEMATICS. *Bolitoglossa jacksoni* is a member of the *B. mexicana* species group (*sensu* Wake and Lynch, 1976) which also includes *B. flaviventris*, *B. mexicana*, *B. mulleri*, *B. odonnelli*, *B. platydactyla*, and *B. salvinii*. The members of the group share a variety of structural and ecological traits; all have the primitive (alpha type) vertebral tail autotomy mechanism (Wake and Dresner, 1967); all have fully webbed feet that lack subdigital pads but have expanded terminal phalanges; all are large species, each represented by specimens exceeding 65 mm standard length; and they occur only in the tropical and low subtropical forests.

The species of the *B. mexicana* group are similar in general structure and have been defined mainly on the basis of coloration. The color patterns of the six species are described below; their geographic ranges are indicated in Figure 7.

Bolitoglossa flaviventris typically has paired dorsolateral light stripes that begin on each eyelid and join to produce a light snout. In the extreme condition, these stripes are paired all the way onto the tail, but often they are irregularly developed and may form a light reticulation, especially posteriorly. This species differs from others with dark flanks in having a light colored and unmarked ventral surface. The light ventral coloration sometimes invades the dorsal surfaces of the legs as well, but the flanks are always dark and sharply set off from the light belly (see Wake and Lynch, 1976, fig. 24). The eye is golden.

Bolitoglossa mexicana has a broad middorsal light swath that is typically broken into three longitudinal stripes by the invasion of dark ground color onto the dorsal surface. The dorsal pattern may range from virtually a single swath (as in *B. platydactyla*) to triple stripes, and then, through loss of the vertebral line, to a bilinear pattern much as seen in *B. odonnelli* (described below). The snout is heavily flecked, and light flecking extends over all of the dark regions of the body (see Wake and Lynch, 1976, frontispiece; Taylor and

Smith, 1945, fig. 58; Stuart, 1943a, plate II, fig. 2). The eye is dark.

Bolitoglossa mulleri typically has a narrow vertebral light stripe. When maximally developed, the stripe extends from the tail tip to the nape of the neck where it bifurcates before terminating on the eyelids. The light pigmentation is frequently reduced, and may be absent altogether leaving a uniformly black animal (see Fig. 5 and Stuart, 1943a, plate II, fig. 4). The eye is dark.

Bolitoglossa odonnelli has narrow paired light stripes. At their maximum development, these stripes extend continuously from the eyelids to the tip of the tail, but frequently they are broken into rows of dots or may not extend as far anteriorly or posteriorly. The body, including the snout, is otherwise unmarked black (see Stuart, 1943a, plate II, fig. 3). The eye is dark.

Bolitoglossa platydactyla has a single broad middorsal light swath on a generally dark ground. The snout is dark and speckled with light flecks; additional flecking may occur on the fore limbs. A light swath begins on the eyelids and extends almost to the tip of the tail (see Wake and Lynch, 1976, fig. 43; Stuart, 1943a, plate II, fig. 1); the eye is dark.

Finally, *B. salvinii* has the same distribution of light dorsal markings as *B. flaviventris*: paired dorsolateral lines that join anteriorly to produce a light-colored snout and that frequently meet across the dorsal midline or break into reticulation. In this species, the ventral surfaces are dark and undifferentiated from the dark flanks, although a light ventral blotch occasionally occurs (see Wake and Lynch, 1976, fig. 24; Schmidt, 1936, fig. 17). The eye may be either light or dark.

Relationships among the *B. mexicana* group species remain obscure. The animals are scarce, and more samples would be needed for a comprehensive analysis of the entire assemblage. While primitive-derived polarities are not understood for the color characters separating the species, the seven taxa cluster in two basic color and pattern groups. Stuart (1943a) considered *B. platydactyla*, *B. mexicana*, *B. mulleri*, and *B. odonnelli* to form a group united by aspects of their coloration, and the remaining three taxa, *B. jacksoni*,

B. flaviventris, and *B. salvinii*, themselves form a cluster. All three of the latter forms have (1) some white edging between dark and light areas; (2) at least some individuals with golden eyes; (3) the same basic hues, yellow (to tan) and chocolate brown; and (4) a dorsal swath of brown bordered bilaterally and on the snout by yellow. These three species are the only members of the *mexicana* group that ever have light ventral coloration (apparently universal in *B. jacksoni* and *B. flaviventris* and occasionally, as small blotches, in *B. salvinii*). An additional unique feature of the *jacksoni*-*flaviventris*-*salvinii* assemblage is that each is marked only with solid colors, the light regions a single uniform yellow and the dark regions an equally pure brown; speckling and mottling are never observed.

ETYMOLOGY. I name this rare and beautiful new species for Jeremy L. Jackson, the friend who aided me in long moldy months of wet season collecting, and the captor of the first, and now sole, representative of this species.

Bolitoglossa lincolni (Stuart, 1943a)

Figure 3

Oedipus lincolni Stuart, 1943a:9.
Magnadigita lincolni: Taylor, 1944:218.
Bolitoglossa lincolni: Wake and Brame, 1963:386.
Bolitoglossa resplendens McCoy and Walker, 1966:1.

TYPE LOCALITY. Monte at Salquil Grande, Depto. El Quiché, Guatemala, 2,450 m elevation.

RANGE. Including the range of *B. resplendens* (herein synonymized with *B. lincolni*), this is one of the widest ranging of Central American salamanders. It occurs on the Pacific Uplands, in the Cuilco, in the Cuchumatanes, and on the Mesa Central de Chiapas. *B. lincolni* is herein reported from one new locality in the Cuchumatanes and one in the Cuilco.

HABITAT AND HABITS. *Bolitoglossa lincolni* were taken in bromeliads and under logs and bark (see Wake and Lynch, 1976, fig. 30). In addition they were found to be active on wet nights. The species occurs in the upper subtropical

Table 2. Summary of geographic variation in *Bolitoglossa lincolni*.

Population	Dorsal pattern	Ventral spotting	Foot webbing	Max. standard length (millimeters)*
Pacific Uplands	Swath to spots	>95% of pop.	Reduced	m 76
				f 74
Cuilco	Swath to spots	<60% of pop.	Intermediate	m 58
				f 79
Cuchumatanes	Swath	>95% of pop.	Extensive	m 66
				f 78
Mesa Central	Swath	>95% of pop.	Reduced	m 62.3**
				f 78.4**

* Males (m), females (f).
** Data from McCoy and Walker (1966).

forest from well above the cloud line up to the lower temperate zone.

SYSTEMATICS. The diagnostic characters differentiating *Bolitoglossa resplendens* from *B. lincolni* are its greater standard length and proportionately shorter limbs. In the description of *B. resplendens* it was reported that a higher incidence of ventral spotting and less extensive interdigital webbing also distinguish *B. resplendens* from *B. lincolni* (McCoy and Walker, 1966).

Examination of specimens from the four known populations indicates that the two supposedly diagnostic features of *B. resplendens* reflect comparison to a limited sample of unusually small *B. lincolni*. Nominate *B. lincolni* from the Cuchumatanes are fully as large as the specimens in the *B. resplendens* type series (McCoy and Walker, 1966) from the Mesa Central de Chiapas (Table 2), and both populations have proportionately longer limbs at smaller standard length (Fig. 8). Specimens from the Cuilco and Pacific Uplands have the same maximum size (Table 2) and limb/body length allometry (Fig. 8) as the other two populations.

Color pattern, both dorsal and ventral, and degree of interdigital webbing vary between the four populations (see Table 2 and Fig. 3 for dorsum of Cuchumatán specimen) but not in concordant patterns that suggest species level differentiation. Thus, I refer the name *Bolitoglossa resplendens* to the synonymy of *Bolitoglossa lincolni*.

Wake and Lynch (1982) reported the results of morphometric and electrophoretic analysis of the *Bolitoglossa franklini* species group. While there is general agreement with my conclusions, they choose to continue to recognize *Bolitoglossa resplendens* as a distinct species based upon the large genetic distance between the Cuilco population and those from the Cuchumatanes and Pacific Uplands. The genetic affinities of the nominate populations of *Bolitoglossa resplendens* on the Mesa Central de Chiapas remain unknown.

Bolitoglossa morio (Cope, 1869)

Figure 3

- Geotriton carbonarius* (part) Cope, 1868:313.
Oedipus morio Cope, 1869:103.
Geotriton morio: Smith, 1877:64.
Spelerpes morio: Boulenger, 1882:70.
Spelerpes bocourti Brocchi, 1883:111.
Magnadigita morio: Taylor, 1944:218.
Magnadigita omniunsanctorum Stuart, 1952:4.
Bolitoglossa omniunsanctorum: Wake and Brame, 1963:386.
Bolitoglossa morio: Wake and Brame, 1963:386.

TYPE LOCALITY. Mountains of Guatemala.

RANGE. This species occurs throughout the Pacific Uplands, in the Chuacús, and in the Cuchumatanes. It is here reported for the first time from the Cuilco.

HABITAT AND HABITS. *B. morio* were taken under logs, in logs, and in bromeliads and were found to be active on rainy nights. They occur in the upper subtropical and lower temperate zone forests between roughly 1,800 and 3,000 m.

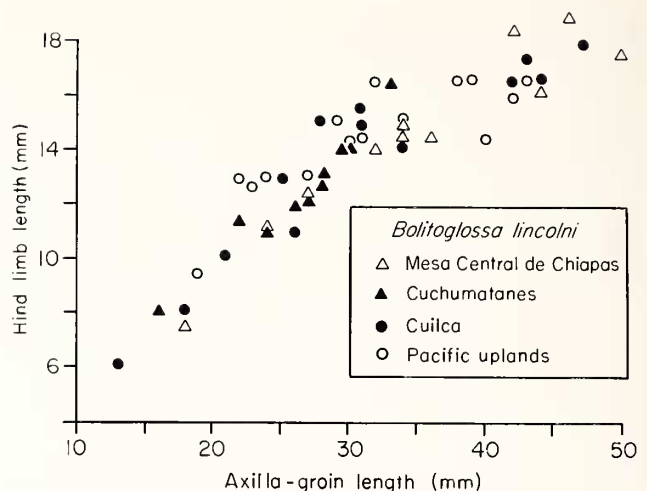


Figure 8. Relationship between hind limb length and axilla-groin length in four populations of *Bolitoglossa lincolni*.

SYSTEMATICS. Relationships of this species are obscure, but its closest relative appears to be *B. flavimembris* (see species group section, below). The characters that unite the populations of this species are the presence of large light (whitish, cream, or pink) blotches on the flanks and/or sides of the tail; the slate grey to brownish ground color of the dorsum; salt and pepper belly mottling; reduced webbing such that all toes of the hind foot are free at their tips; and the robust body form.

The newly discovered Cuilco population has all of the specific characters, except that the lateral markings are reduced to small flecks (diameters less than that of the eye), which are restricted to the sides of the tail rather than extending onto the trunk.

Bolitoglossa mulleri (Brocchi, 1883)

Figure 5

- Spelerpes mulleri* Brocchi, 1883:116.
Oedipus platydactylus (part) Dunn, 1926:400.
Oedipus mulleri: Schmidt, 1936:150.
Bolitoglossa mulleri: Taylor, 1944:219.
Oedipus mexicanus mulleri: Stuart, 1948:19.
Bolitoglossa moreleti mulleri: Duellman, 1963:220.
Bolitoglossa mexicana mulleri: Wake and Brame, 1963:386.

TYPE LOCALITY. Several localities in Alta Verapaz, restricted by Stuart (1943a) to "les montagnes qui dominant Coban."

RANGE. This form had been taken only in the Xucaneb complex until discovered in the Cuchumatanes during the study described here. It is now known from Santa Cruz Barillas and from a finca 3 km to the NE at 1,500 m (Fig. 7).

HABITAT AND HABITS. This species occurs in the low pine-broadleaf cloud forest border in the Xucaneb and was found in the Cuchumatanes in the cutover Barillas valley, which was once a mix of the two forest types. This area is at the elevation of the lower subtropical zone but is drier

because of its protected position. Of the ten or so specimens taken from the Cuchumatanes, all but one were found under stones in a well-watered garden in the town of Barillas. The other specimen was found under a piece of wood in a stand of coffee. In the Xucaneb the species has been taken between 1,000 and 1,500 m.

SYSTEMATICS. The new population has a somewhat reduced middorsal light stripe relative to animals from the type locality: markings never extend anterior to the nape, and some individuals are unmarked black.

Bolitoglossa mulleri is a member of the *Bolitoglossa mexicana* species group (*sensu* Wake and Lynch, 1976). Variation and relationships among the *mexicana* group species are discussed in the *B. jacksoni* account above.

Bolitoglossa rostrata (Brocchi, 1883)

Figure 3

Spelerpes rostratum Brocchi, 1883:112.

Oedipus rostratum: Dunn, 1924:99.

Oedipus rostratus: Dunn, 1926:384.

Magnadigita rostrata: Taylor, 1944:218.

Bolitoglossa rostrata: Wake and Brame, 1963:386.

TYPE LOCALITY. The mountains of Totonicapan, Guatemala.

RANGE. This species is one of the most broadly ranging forms in Nuclear Central America, from the Mesa Central de Chiapas through the Cuchumatanes and into the Pacific Uplands. A newly discovered population at the eastern extremity of the Cuchumatanes indicates that the species may be distributed throughout that cordillera.

HABITAT AND HABITS. *B. rostrata* were taken in and under logs, under bark, in bunchgrass, and under rocks, and were found to be active on rainy nights. The species occurs only above 2,700 m and up to about 3,000 m, in temperate forests and above the treeline in bunchgrass associations.

SYSTEMATICS. The species is distinguished by the following characters: it has almost unwebbed toes (as unwebbed as any member of the genus); it is brown, typically with a middorsal swath of light color or light shoulder stripes; and it has a uniform light beige to dull yellow ventral and subcaudal color.

B. rostrata appears to be most closely related to the *B. dunni* series (see *B. cuchumatana* account above) and where it occurs in sympatry with *B. cuchumatana* the two species are separated with difficulty. *Bolitoglossa rostrata* is distinguishable from *B. cuchumatana* on a number of subtle characters; it occurs in an unstriped morph, is slightly less robust, has a longer tail, and shows reduced interdigital webbing (Fig. 3).

Bolitoglossa rufescens (Cope, 1869)

Figure 5

Oedipus rufescens Cope, 1869:104.

Geotriton rufescens: Smith, 1877:76.

Spelerpes rufescens: Boulenger, 1882:71.

Bolitoglossa rufescens: Taylor, 1941:145.

Palmatotriton rufescens: Smith, 1945:4.

TYPE LOCALITY. Orizaba, Veracruz, Mexico.

RANGE. The range of this species is broad, extending along the Atlantic versant throughout western Honduras, Guatemala, and Chiapas, Mexico, and continuing up the Atlantic coastal plain through the Mexican state of Veracruz to San Luis Potosi. The species is well known from Chiapas and the low Xucaneb on both sides of the Cuchumatanes, but this is the first report of its occurrence in the Cuchumatanes proper. It occurs just below the cloud line at Finca Chiblac in the northwestern Cuchumatanes.

HABITAT AND HABITS. This species almost always occurs in the leaf bases of banana plants. All but one of the four *B. rufescens* taken in the Cuchumatanes were found in this situation. The exception was found crossing a trail on a sultry, overcast afternoon at about 1400 h. The species occurs throughout the tropical zone forest from near sea level (Stuart, 1943a) up to the 1,200-m cloud line.

SYSTEMATICS. Specimens from the Cuchumatanes were assigned to *B. rufescens* based upon derived skull and foot structure and the absence of maxillary teeth.

Bradytriton silus Wake and Elias, 1983

Figure 9

Bradytriton silus Wake and Elias, 1983:3.

TYPE LOCALITY. Finca Chiblac, 15 km NE Barillas, Huehuetenango, Guatemala, elevation 4,300 ft. (1,310 m).

RANGE. This species was discovered in the course of this investigation. It is known only from the type locality.

HABITAT AND HABITS. Eleven of the twelve known specimens were taken beneath pieces of wood in a clearing that was being prepared for the cultivation of quinine. The other individual was found under a log in the undisturbed subtropical zone cloud forest surrounding the clearing. The native forest at the type locality is a mixed hardwood growth that receives over 6 m of rain yearly.

SYSTEMATICS. This species has unique specializations and has been placed in a monotypic genus. Its possible relationships are discussed by Wake and Elias (1983).

Dendrotriton cuchumatanus (Lynch and Wake, 1975)

Figure 5

Chiropterotriton cuchumatanus Lynch and Wake, 1975:6.

Dendrotriton cuchumatanus: Wake and Elias, 1983.

TYPE LOCALITY. On highway 9N, 8.5 km (by road) SW San Juan Ixcay, Depto. Huehuetenango, Guatemala, elevation 2,860 m.

RANGE. This species is known only from the type locality. Appropriate habitat is present elsewhere in the area, and this species may range more widely than is presently known.

HABITAT AND HABITS. This species has been taken under moss and bark on large fallen trees. The type locality is a patch of great buttressed rain forest oaks on the sub-

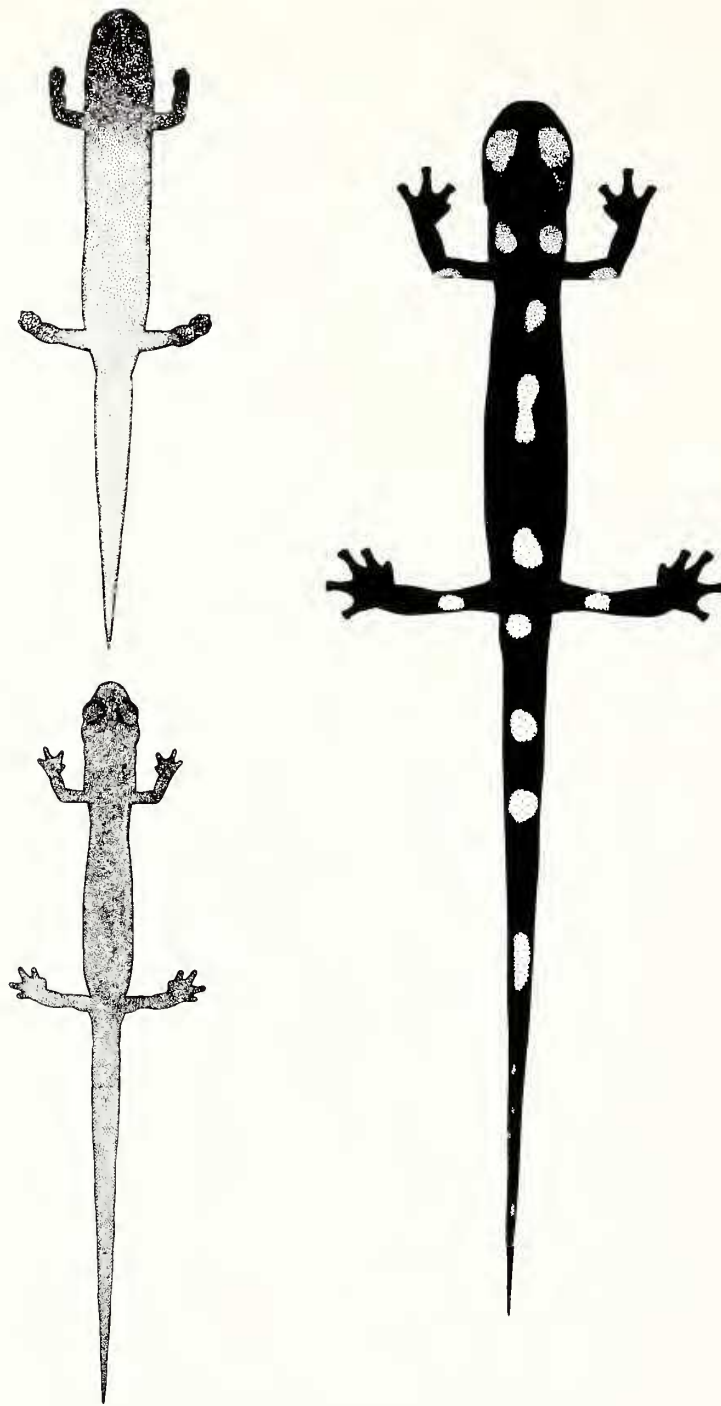


Figure 9. *Bradytriton silus*, *Pseudoeurycea rex*, and *Nyctanolis pernix*, life size. UPPER LEFT: *Bradytriton silus*, head, legs, and feet slate grey, trunk and tail brick red-brown. LOWER LEFT: *Pseudoeurycea rex* (Cuchumatan specimen), dark brown overall (in some Cuchumatan specimens and in most Cuilco animals, there is light speckling, especially laterally). RIGHT: *Nyctanolis pernix*, background color black, spots on eyelids and nape crimson, those on elbows and knees orange, trunk and tail spots yellow.

tropical-temperate zone border. This area receives a great but undetermined amount of precipitation both in the form of rain and as dense, cold fog.

SYSTEMATICS. The genus *Dendrotriton* has been reviewed by Lynch and Wake (1975). Their results suggest close relationship between *D. cuchumatanus*, *D. bromeliacea*, and

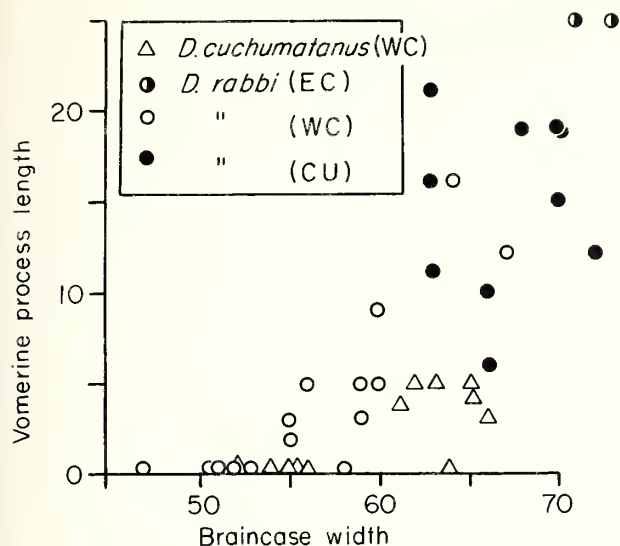


Figure 10. Relationship between length of the preorbital process of the vomer and braincase width in *Dendrotriton rabbi* and *D. cuchumatanus* (in micrometer units). WC = Western Cuchumatanes; EC = Eastern Cuchumatanes; CU = Cuilco.

D. megarhinus (the latter two are inhabitants of the Pacific Uplands), based upon shared configurations of the vomer and the nostril.

Dendrotriton rabbi (Lynch and Wake, 1975)

Figure 5

Chiropterotriton rabbi Lynch and Wake, 1975:2.

Dendrotriton rabbi: Wake and Elias, 1983.

TYPE LOCALITY. 9.5 km W, 8.5 km S (by air) La Democracia, Depto. Huehuetenango, Guatemala, elevation 2,100 to 2,500 m.

RANGE. This species, described and hitherto known only from a spur of the Montañas de Cuilco, is here reported both from the main massif of the Cuilco and from two localities in the Cordillera de los Cuchumatanes.

HABITAT AND HABITS. *Dendrotriton rabbi* occur at the subtropical-temperate border. In the Cuilco, they have most frequently been found in bromeliads but only under bark on logs and stumps in the Cuchumatanes, perhaps because bromeliads are absent from the appropriate elevations. The species occurs from 2,100 to 2,700 m.

SYSTEMATICS. The newly discovered populations have been referred to *D. rabbi* on the basis of a small nostril diameter and the presence of a preorbital process on the vomer in adults (as distinct from *D. cuchumatanus*, *D. bromeliacea*, and *D. megarhinus*) and because some specimens from each population have ossified septomaxillary bones (absent in *D. xolocalcae*) (for discussion, see Lynch and Wake, 1975, 1978).

Lynch and Wake (1975) examined the ontogeny of the nostril in all of the species of *Dendrotriton* and discovered that all juveniles have similar, relatively large nostrils. They found that patterns of relative growth determined the adult

condition; species that as adults have small nostrils experience either no growth or actual shrinkage in the absolute size of the nostril through ontogeny, while large nostriled forms experience nostril growth.

I have examined ontogenetic variation in the presence or absence of the preorbital process of the vomer. The process is large and tooth-bearing in small nostriled species but, if present, is a nub in species with large nostrils. As with nostril size, vomerine process length is initially equal in the large nostriled *D. cuchumatanus* and small nostriled *D. rabbi*. Differential growth produces the difference in the adult condition in the two species (Fig. 10). In this case, interspecific differences are compounded by a differential in maximum adult size. These data further indicate that the newly discovered Cuchumatán populations clearly fall with the nominate *D. rabbi*. With the new localities reported here, *D. rabbi* is known to occur within 250 vertical m and about 25 km of *D. cuchumatanus* in the Cuchumatanes. The two species have been taken in similar habitats without intervening ecological barriers, and the proximity of the two suggests that the first case of sympatry in the genus may yet be found.

Nyctanolis pernix Elias and Wake, 1983

Figure 9

Nyctanolis pernix Elias and Wake, 1983:2.

TYPE LOCALITY. Finca Chiblac, about 10 km NE Santa Cruz Barillas, Depto. Huehuetenango, 1,370 m (4,500 ft.) elevation.

RANGE. This species has been taken at the type locality, just across the Mexican border in Chiapas and in the western end of the Sierra de las Minas near Purulhá, Baja Verapaz (J. Campbell, pers. comm.).

HABITAT AND HABITS. The type series was found under moss and bark during the day and on stumps and logs on wet nights. The type locality is a region of quinine cultivation in the subtropical zone, just above the cloud line. The forest receives over 6 m of rain annually. The Mexican specimen was taken in the mouth of a cave in the cloud forest.

SYSTEMATICS. This species was discovered during the course of this investigation and appears to have no close relatives. The relationships of this monotypic genus were discussed by Elias and Wake (1983).

Pseudoeurycea rex (Dunn, 1921)

Figure 9

Oedipus rex Dunn, 1921:143.

Pseudoeurycea rex: Taylor, 1944:209.

TYPE LOCALITY. Sierra Santa Elena (near Tecpam), Guatemala, elevation 9,500 ft. (2,900 m).

RANGE. *P. rex* is known from the Cuchumatanes and from several regions on the Pacific Uplands. The species is here recorded for the first time from the Montañas de Cuilco.

HABITAT AND HABITS. This form occurs from 2,750 m elevation to over 4,000 m at the top of the highest moun-

tains in its range and occurs in the temperate zone forest and above the treeline in open bunchgrass communities. They live under and within logs, under bark, moss, grass clumps, and stones and were found active in the open on wet nights. *P. rex* is often abundant, reaching densities higher than those of any other Guatemalan salamander.

SYSTEMATICS. The Guatemalan members of the genus *Pseudoeurycea* are four or five similar brown to black-colored species. Species-level differences in foot webbing and color pattern have proven difficult to document and tend to be exceeded by intrapopulational variation. No careful quantitative work on variation in this assemblage has been published, and my allocation of the Cuilco and Cuchumatán populations is based upon their elevational distribution and their general morphological similarities to known populations of *P. rex*.

DISCUSSION

SPECIES GROUPS IN *BOLITOGLOSSA* BETA

Since Wake and Lynch (1976) last outlined species groups in the genus *Bolitoglossa*, examination of new material from the Cuchumatanes, the Cuilco, the Pacific Uplands, and the Sierra de las Minas has blurred certain distinctions and clarified others among the species found in Nuclear Central America (abbreviated NCA and including the entire land-mass between the Isthmus of Tehuantepec and the Nicaraguan Depression). Implicit in some of the comparisons made in the preceding species accounts, and crucial to the discussion sections to come, is a revision of the species groups for Guatemalan *Bolitoglossa*.

Wake and Dresner (1967) found that a group of derived structural characters involved in tail autotomy was shared by certain species of *Bolitoglossa*. The derived group, referred to by Wake and Lynch (1976) as "*Bolitoglossa* beta," includes all Mexican and NCA species except the *B. mexicana* group, as well as two forms from the Talamancan highlands further south. Included are the following species: *B. alvaradoi*, *B. arboroscandens*, *B. cuchumatana*, *B. dofleini*, *B. dunni*, *B. engelhardti*, *B. flavimembris*, *B. franklini*, *B. hartwegi*, *B. helmrichi*, *B. lincolni*, *B. macrinii*, *B. melania*, *B. morio*, *B. occidentalis*, *B. riletti*, *B. rostrata*, *B. rufescens*, *B. schmidtii*, *B. stuarti*, *B. veracrucis*, *B. yucatanana*, and at least one undescribed species (Wake and Lynch, 1982).

Species groups within *Bolitoglossa* beta were first recognized informally. Taylor (1941), in his description of *B. occidentalis*, noted the affinity between his new species and *B. rufescens*. Stuart (1943a) noted that *B. dofleini* and *B. yucatanana* were close relatives. He also suggested that *B. cuchumatana*, *B. dunni*, *B. engelhardti* and *B. helmrichi* formed a close group in terms of both morphology and ecology, and in a later paper (1952) he named them the *B. dunni* species group. In the description of *B. lincolni* Stuart (1943a) reported the new species to be most closely affiliated with *B. franklini* on morphological grounds, and later (Stuart, 1952) included them with the then newly described *B. nigroflavescens* in a *B. franklini* species group. Recently Wake and Lynch (1982) reduced *B. nigroflavescens* to the status of a subspecies

within *B. franklini*. Stuart (1952) erected the *B. morio* group to contain *B. morio* and *B. omniunssanctorum*, but Wake and Elias (1983) synonymized the two.

By 1952, therefore, five species assemblages had been recognized within *Bolitoglossa* beta, leaving unassigned only the following six of the nineteen species then known: *B. flavimembris*, *B. macrinii*, *B. riletti*, *B. rostrata*, *B. schmidtii* and *B. veracrucis* (see Table 3). Wake and Brame (1969) named two new species, *B. hartwegi* and *B. stuarti*, and demonstrated their close morphological similarities to one another and to *B. veracrucis*. In addition they reorganized Stuart's (1943a, 1952) three species groups into two new ones, the *B. rostrata* and *B. helmrichi* groups (Table 3). These two groups were large and heterogeneous as compared to those described above. The *B. rostrata* group included Stuart's (1952) *B. morio* and *B. franklini* groups, *B. dunni* and *B. engelhardti* from his *B. dunni* group, the previously unassigned *B. macrinii*, *B. riletti* and *B. rostrata*, and the recently described species *B. resplendens* and *B. brevipes*. Their *B. helmrichi* group included *B. cuchumatana* and *B. helmrichi* from Stuart's (1952) *B. dunni* group, the previously unassigned *B. flavimembris* and *B. veracrucis*, and the new species *B. hartwegi* and *B. stuarti*.

Wake and Lynch (1976) assembled the first complete listing of *Bolitoglossa* species groups. They tentatively assigned every species to some group and recognized a total of six species groups within *Bolitoglossa* beta. The *B. dofleini* group was erected to include *B. dofleini*, *B. yucatanana* and the poorly known *B. schmidtii*. The *B. rufescens* group was recognized as containing *B. occidentalis* and *B. rufescens*. The two Talamancan species from southern Central America, *B. alvaradoi* and *B. arboroscandens*, were placed together in a *B. alvaradoi* group, and the two species from north of the Isthmus of Tehuantepec, *B. macrinii* and *B. riletti*, were put in a *B. macrinii* group. The two large groups, *B. rostrata* and *B. helmrichi*, of Wake and Brame (1969), were retained with their original membership but for the switching of *B. morio* from one to the other and the inadvertent omission of *B. omniunssanctorum* altogether (see Table 3).

The recognition of polyphyletic groups (groups united by characters not shared by their most recent common ancestor) is a severe obstacle to phylogenetic reconstruction. Ensuring that only nonpolyphyletic (= paraphyletic and monophyletic) species groups are recognized is a first step towards an understanding of the phylogenetic history of *Bolitoglossa* beta. To eliminate possibly polyphyletic groups I have recognized only tight clusters of phenotypically similar species. Morphological similarity between species group members is demonstration of nonpolyphyletic origin of the group insofar as such similarities are homologous (acquired by descent from a similarly endowed common ancestor).

The *B. rostrata* and *B. helmrichi* groups of Wake and Lynch (1976) are large, heterogeneous and united by no specific characters. To compose tighter units more comparable to other species groups in *Bolitoglossa* beta I have subdivided and reorganized these two groups.

The *B. rostrata* group contains a series of species that has been recognized as a phenetic cluster by many authors (Stuart,

Table 3. The species groups of *Bolitoglossa* beta as defined by different authors. Species not assigned to a group until after 1952 (both newly described and described but previously unaffiliated species) are indicated by an asterisk where they first appear.

Early classifications	Wake and Brame, 1969	Wake and Lynch, 1976	Elias, 1983	
Stuart, 1952	<i>*hartwegi</i> <i>*stuarti</i> <i>*veracrucis</i> <i>cuchumatana</i> <i>helmrichi</i> <i>flavimembris</i> helmrichi group <i>dunni</i> <i>engelhardii</i> <i>*rostrata</i> <i>morio</i> <i>omniumsanctorum</i> <i>*resplendens</i> <i>franklini</i> <i>lincolnii</i> <i>nigroflavescens</i> <i>brevipes</i> rostrata group <i>dunni</i> <i>engelhardii</i> <i>engelhardii</i> <i>*macrinii</i> <i>*riletti</i>	<i>hartwegi</i> <i>stuarti</i> <i>veracrucis</i> <i>cuchumatana</i> <i>helmrichi</i> <i>morio</i> <i>flavimembris</i> helmrichi group <i>dunni</i> <i>engelhardii</i> <i>rostrata</i> rostrata group <i>macrinii</i> <i>riletti</i> macrinii group <i>dofleini</i> <i>yucatanana</i> <i>*schmidti</i> dofleini group <i>*alvaradoi</i> <i>*arboroscandens</i> alvaradoi group <i>occidentalis</i> <i>rufescens</i> rufescens group	<i>hartwegi</i> <i>stuarti</i> <i>veracrucis</i> <i>cuchumatana</i> <i>helmrichi</i> veracrucis group <i>dunni</i> <i>engelhardii</i> <i>rostrata</i> dunni group <i>morio</i> <i>flavimembris</i> morio group <i>franklini</i> <i>lincolnii</i> <i>*melania</i> franklini group <i>macrinii</i> <i>riletti</i> macrinii group <i>dofleini</i> <i>yucatanana</i> <i>schmidti</i> dofleini group <i>alvaradoi</i> <i>arboroscandens</i> alvaradoi group <i>occidentalis</i> <i>rufescens</i> rufescens group	<i>hartwegi</i> <i>stuarti</i> <i>veracrucis</i> <i>cuchumatana</i> <i>helmrichi</i> veracrucis group <i>dunni</i> <i>engelhardii</i> <i>rostrata</i> dunni group <i>morio</i> <i>flavimembris</i> morio group <i>franklini</i> <i>lincolnii</i> <i>*melania</i> franklini group <i>macrinii</i> <i>riletti</i> macrinii group <i>dofleini</i> <i>yucatanana</i> <i>schmidti</i> dofleini group <i>alvaradoi</i> <i>arboroscandens</i> alvaradoi group <i>occidentalis</i> <i>rufescens</i> rufescens group
	<i>dofleini</i> <i>yucatanana</i>	<i>dofleini</i> <i>yucatanana</i> <i>*schmidti</i> dofleini group	<i>dofleini</i> <i>yucatanana</i> <i>schmidti</i> dofleini group	
Dunn, 1926	<i>*macrinii</i> <i>*riletti</i>	<i>macrinii</i> <i>riletti</i> macrinii group	<i>macrinii</i> <i>riletti</i> macrinii group	
	<i>dofleini</i> <i>yucatanana</i>	<i>dofleini</i> <i>yucatanana</i> <i>*schmidti</i> dofleini group	<i>dofleini</i> <i>yucatanana</i> <i>schmidti</i> dofleini group	
Taylor, 1941	<i>occidentalis</i> <i>rufescens</i> rufescens group	<i>*alvaradoi</i> <i>*arboroscandens</i> alvaradoi group <i>occidentalis</i> <i>rufescens</i> rufescens group	<i>alvaradoi</i> <i>arboroscandens</i> alvaradoi group <i>occidentalis</i> <i>rufescens</i> rufescens group	

1943a, 1952, as his *B. franklini* group; McCoy and Walker, 1966, Wake and Brame, 1969, and Wake and Lynch, 1976, as the *B. lincolni* subgroup of their *B. rostrata* group; Wake, Yang, and Papenfuss, 1980, and Wake and Lynch, 1982, as the *B. franklini* species group). This assemblage includes *B. franklini*, *B. lincolni*, *B. melania*, and one undescribed Chiapan form (Wake and Lynch, 1982, who also include *B. resplendens*). These species are characterized by large adult size, stout bodies and tails, and a black ground color broken dorsally only by a sharply bounded swath, spotting, or reticulation in some lighter color; red in some species to yellow or grey-green in others (see *B. lincolni*, Fig. 3). *B. melania* is solid black. These species all have toetips free of webbing and subdigital pads. They are distributed allopatrically except for an area of elevational parapatry with occasional hybridization between the high elevation *B. lincolni* and lower elevation *B. franklini* on the Pacific Uplands (Wake, Yang, and Papenfuss, 1980).

The remainder of the *B. rostrata* group of Wake and Lynch (1976), including *B. dunni*, *B. engelhardti* and *B. rostrata*, fits with *B. cuchumatana* and *B. helmrichi* of their *B. helmrichi* group to form an assemblage characterized by blunt rounded toetips, fully developed subdigital pads, and a dark brown ground color, frequently marked with a lighter brown dorsal swath or paired shoulder stripes (see *B. rostrata* in Fig. 3 for typical color pattern and compare *B. rostrata* and *B. cuchumatana* [inset] feet as examples of variation in foot morphology within the group). Stuart (1943a, 1952) recognized this assemblage as his *B. dunni* group but hesitated to include *B. rostrata* because of its different ecology. Relying on morphological similarities, I recognize this assemblage, including *B. rostrata*, as a new *B. dunni* species group. The members of the *B. dunni* group are all either geographically or elevationally (in the case of *B. rostrata* and *B. engelhardti* in the Pacific Uplands) allopatric, except that narrow sympatry is seen between the high elevation *B. rostrata* and the lower *B. cuchumatana* in the Cuchumatanes.

Bolitoglossa hartwegi, *B. stuarti*, and *B. veracruzis* were recognized by Wake and Brame (1969) to form a compact subgroup within their *B. helmrichi* group. I choose to recognize the similarities of these species by isolating them in a new *B. veracruzis* species group. The three species are united by the combination of fully webbed feet that lack subdigital pads and are differentiated from members of the *B. rufescens* group by possession of a strongly articulated skull with a broad pars dentalis of the premaxilla. The *B. veracruzis* group has the broadest elevational range of any group of NCA salamanders (see elevational distribution section below), and no two species occur sympatrically.

The two remaining species left over from Wake and Lynch's (1976) *B. helmrichi* group are *B. flavimembris* and *B. morio*. *B. morio* is slightly larger than *B. flavimembris*, but the two share a stout body and tail and a unicolor dorsum (see *B. morio* in Fig. 3). That *B. flavimembris* is not affiliated with the *B. dunni* group is indicated both by its coloration and build and by its rather pointed toetips and poorly developed subdigital pads (see Wake and Lynch, 1976, fig. 22). New evidence that *B. morio* and *B. flavimembris* are relatives

comes from the discovery of populations of intermediate morphology in the Pacific Uplands of Guatemala near the Mexican border (D.B. Wake, pers. comm.). Given these indications of relationship, and the absence of other affiliations, I group *B. flavimembris* and *B. morio* together in a new *B. morio* species group.

Aside from the changes proposed above I follow the species group assignments of Wake and Lynch (1976); the full history of species groups among the species of *Bolitoglossa* beta including my revisions is presented in tabular form in Table 3.

PATTERNS OF DISTRIBUTION AND DIFFERENTIATION

Faunal Connections Between the Mexican Plateau, NCA, and the Talamancas

Wake and Lynch (1976) found that the three most mountainous areas of Middle America are especially high in salamander species diversity; these are the Caribbean escarpment of the Mexican Plateau, the mountains of NCA, and the Talamancan highlands of Costa Rica and Panama. That there has been faunal contact between these centers of diversity is demonstrated by the distribution of some genera on more than one of the three upland areas. For example, the NCA fauna includes some genera that range to the Mexican Plateau (*Pseudoeurycea*), others that range to the Talamancas (*Oedipina* and *Nototriton*), still others that occur on all three upland areas (*Bolitoglossa*), as well as genera endemic to NCA (*Bradytriton*, *Dendrotriton*, and *Nyctanolis*). Each genus has a clear center of intrageneric diversity on one of the three upland regions (except *Bolitoglossa*, in which the alpha and beta subgeneric groups center on two different uplands (Wake and Lynch, 1976)). This pattern suggests that most intrageneric evolution proceeded on single upland areas at a time when the three major uplands were isolated from one another.

If we go one step further back, however, and consider the origins of the genera themselves, we find that genera with distributions centered on the same upland area (i.e., *Bradytriton*, *Dendrotriton*, *Nyctanolis*, and the beta complex of *Bolitoglossa* in NCA) do not usually form a clearcut monophyletic group (Wake and Elias, 1983). This implies a complex history of ancient faunal contact between the three great upland regions of Middle America.

Faunal Connections Among the Mountain Ranges of NCA

Within NCA, the uplands form discrete islands of habitat for high elevation salamander species. Between these uplands lie warmer, drier, rain-shadowed valleys that are generally uninhabited by salamanders. Around the coastward periphery of these mountains are warm, humid lowlands that support a restricted plethodontid fauna. Most of the salamanders occurring in NCA are montane (including *Bradytriton*, *Dendrotriton*, *Nototriton*, *Nyctanolis*, and *Pseudoeurycea*). A single genus, *Oedipina*, is restricted to the lowlands. Only *Bolitoglossa* occurs at all elevations, and even this genus is split

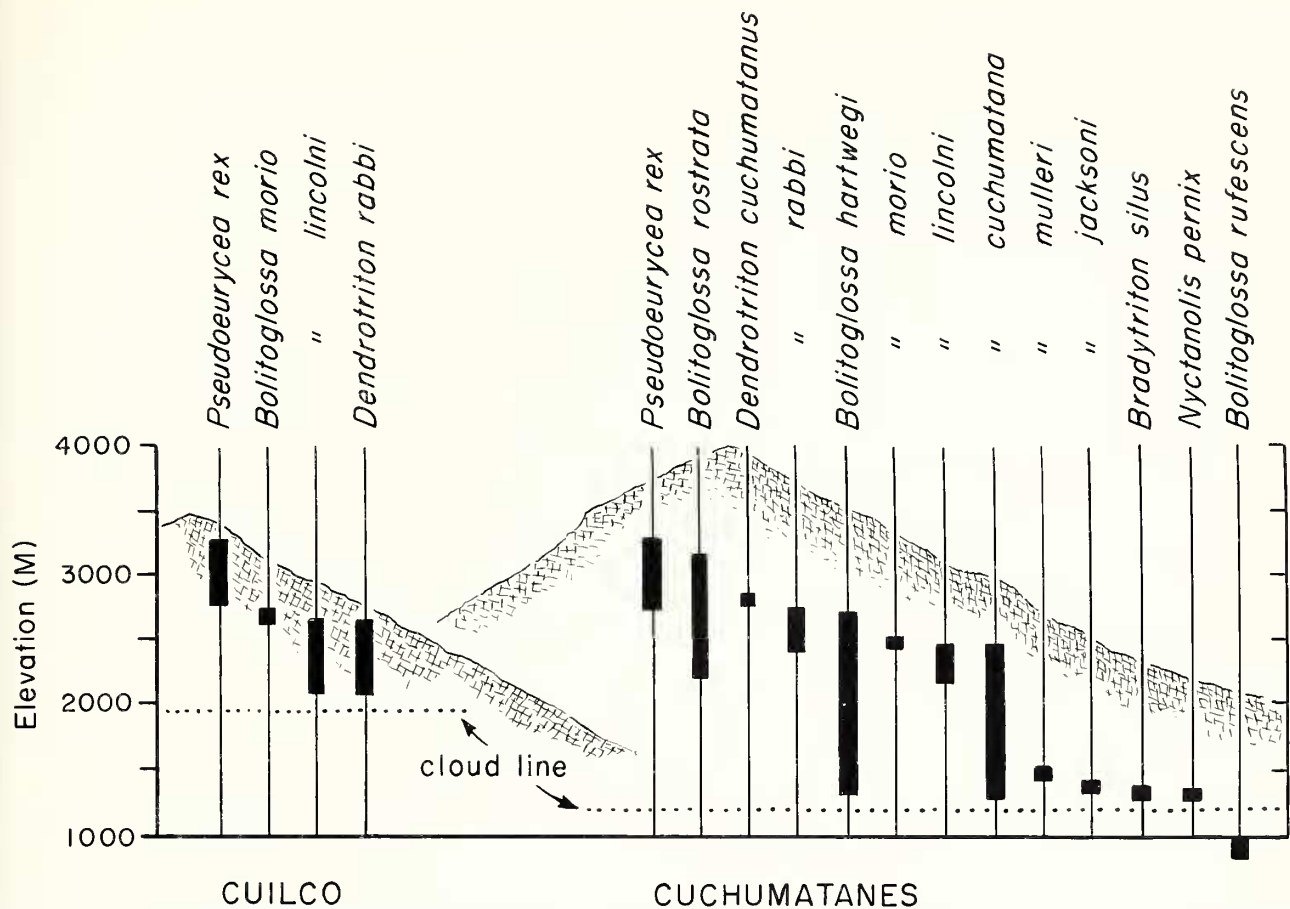


Figure 11. Elevational distribution of salamander species on the Montañas de Cuilco and the Cordillera de los Cuchumatanes (all collections combined).

into upland (*B. helmrichi*, *B. morio*, *B. franklini*) and lowland (*B. mexicana*, *B. dofleini*, *B. rufescens*) species assemblages (the *B. veracruensis* group is exceptional in its broad elevational range and will be discussed separately below). The upland and lowland faunas intermingle narrowly in the low cloud forest at about 1,000 m elevation, but the upland groups are subject to special biogeographic limitations, which give their current patterns of differentiation particular historical interest.

Comparison of patterns of upland diversity obtaining in the Cuchumatanes relative to the Pacific Uplands raises interesting contrasts. There are fifteen upland salamander species known from the Pacific Uplands (Wake and Lynch, 1976, 1982) and only nine (excluding *B. hartwegi* of the *B. veracruensis* group) from the Cuchumatanes, but the supraspecific diversity is greater in the Cuchumatanes. The nine Cuchumatane species belong to five genera, and the four *Bolitoglossa* fall into three species groups. In the Pacific Uplands, however, the fifteen species are in three genera, and all seven *Bolitoglossa* are in the same three species groups that occur in the Cuchumatanes. No genus or species group in the Pacific Uplands is not also represented in the Cuchumatanes, but two genera present in the Cuchumatanes are absent in the Pacific Uplands. The two areas have four species in common:

Bolitoglossa lincolni (here including *B. resplendens*), *B. morio*, *B. rostrata*, and *Pseudoeurycea rex*.

The fact that salamander diversity is so deep in the Cuchumatanes may reflect that region's ancient history as a land-positive area (Rosen, 1978).

The shallowness of salamander diversity on the Pacific Uplands may reflect the topography of that area: the highlands are composed of many abutting cinder cones. Small climatic fluctuations should have caused alternate fragmentation and reunion of the geographic ranges of highland salamander species. When a species' range is subdivided and then reunified after a period in this way, a complex of introgressions, parapatrics and sympatrics might be expected to result as partially differentiated sister populations are thrown back into contact after a period of allopatry on neighboring cinder cones. Just these sorts of interactions are found among the Pacific Uplands salamanders (Wake and Lynch, 1976; Wake, Yang, and Papenfuss, 1980; Wake and Lynch, 1982).

ELEVATIONAL DISTRIBUTION

Schmidt (1936) documented the elevational ranges of salamander species along a transect down the coastal escarpment

of the Pacific Uplands. He found that species there inhabited narrow, sharply bounded elevational ranges and that a given species typically inhabited similar elevations at different transect sites along the Pacific escarpment.

Wake and Lynch (1976) performed a detailed analysis of elevational distribution along a transect near the volcano first studied by Schmidt. They corroborated Schmidt's results and filled them out with detailed studies of elevational boundary zones and possible interspecific competition.

Composite transects (grouping all collections) for the Cuchumatanes and Cuilco (Fig. 11) compared to the transect results of Wake and Lynch (1976) for Volcan Tajumulco in the Pacific Uplands indicate that related populations (either conspecifics or members of related species) show similar elevational ranges wherever they occur. Many of the related populations that have significant variation in elevational distribution between transects appear to vary in response to geographic variation in the elevation of the cloud line.

The results for the Cuchumatanes and Cuilco reinforce the generalization that salamander populations in NCA inhabit narrow elevational belts, and recent information for all uplands in NCA indicates that with one exception no single species or group of related species (meaning species groups in *Bolitoglossa* and entire genera in other cases) occurs over an elevational range as broad as 1,300 m. The exception is *Bolitoglossa hartwegi* (with a 1,500-m elevational range) and the *Bolitoglossa veracruzis* species group with a combined elevational range of over 2,800 m. As Wake and Brame (1969) have pointed out, and as these results reiterate, this exceptional group may have played a key role in the invasion of the lowlands by *Bolitoglossa* beta and must have unique physiological attributes, which, if studied, might expand our understanding of the history of salamanders throughout Middle America.

SPECIMENS EXAMINED

Salamanders are known from the following localities in the Cordillera de Los Cuchumatanes, Depto. Huehuetenango, and the Sierra de Cuilco, Depto. Quiché, Guatemala.

Bolitoglossa cuchumatana. CUCHUMATANES. Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 1,300–1,500 m, 3 km S of buildings, MVZ 134524–72, 134574–79, 134582–88, LACM 135482–85; El Porvenir, 134603–16; Finca Chiblac, 149306–14; 1.5 km S of buildings, 134591–602; San Isidro, 134617–22; El Rayo, 134623–25. On ridge ca. 4 km (airline) NW Santa Cruz Barillas, el. 2,000 m, MVZ 149315.

CUILCO. 6.7 mi. (rd.) S Nebaj on Rta. Depto. 3, el. 2,500 m, MVZ 160993–1005. On ridge 2.5 km W, 2 km N (airline), San Miguel Uspantán, el. 2,200–2,500 m, MVZ 149301–05. Oak forest about 2 km (airline) N Nebaj, el. 1,900 m, UMMZ 89110 (holotype), 89111–13.

Bolitoglossa hartwegi. CUCHUMATANES. Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 1,300–

1,500 m, MVZ 134629, 134631–33, LACM 135481; 3 km S of buildings, MVZ 149324. 3 km (airline) NNW San Mateo Ixtatán, el. 2,750 m, MVZ 160355–59.

CUILCO. On ridge 2.5 km W, 2 km (airline) N San Miguel Uspantán, el. 2,200–2,500 m, MVZ 149325.

Bolitoglossa jacksoni. CUCHUMATANES. Finca Chiblac, ca. 12 km (airline) NE Santa Cruz Barillas, el. 1,400 m, MVZ 134634 (holotype).

Bolitoglossa lincolni. CUCHUMATANES. Just N San Juan Ixcay, UMMZ 123275–76. Ca. 9 mi. (rd.) SW El Reposo, summit between El Reposo and Oja Blanca, el. 2,200–2,300 m, MVZ 161791, 119011. Planes de Peña Blanca, 1.5 km (airline) NE Peña Blanca peak, el. 2,700 m, MVZ 149359–64; 9.5 km W, 8.5 km (airline) S, La Democracia, el. 2,100–2,500 m, MVZ 103834–38; 10 km W, 143681–87. Paraiso Hoja Blanca Cumbre, UMMZ 129149–50.

CUILCO. Monte at Salquil Grande, el. 2,450 m, UMMZ 89107 (holotype), 89108–09. On ridge NW San Miguel Uspantán, el. 2,200–2,500 m, 2.5 km N Uspantán, MVZ 149365–69; 3.5 km (air) NNW, 160833–39.

Bolitoglossa morio. CUCHUMATANES. Planes de Peña Blanca, 1.5 km (airline) NE Peña Blanca peak, el. 2,700 m, MVZ 149335–43. Todos Santos, el. 2,500 m, UMMZ 102285–86 (holotype and paratype of *Oedipus omnium-sanctorum*).

Bolitoglossa mulleri. CUCHUMATANES. Town of Santa Cruz Barillas, el. 1,500 m, MVZ 131691–93, 149327–31, 161102. Finca la Florida ca. 2 mi. (rd.) NE Santa Cruz Barillas, el. 1,500 m, MVZ 149326.

Bolitoglossa rostrata. CUCHUMATANES. Ca. 37–40 km (rd.) N Huehuetenango, el. 2,860 m, MVZ 113418–540. Vicinity Capzín, Rta. Nac. 9N, 50–60 km (rd.) N Huehuetenango, el. 2,800–3,200 m, 52.7 km N, MVZ 114722–65; ca. 50 km N, km post 139, 115494–524, 117039. 2–8 km N, W, and S (airline) San Mateo Ixtatán, el. 2,700–3,200 m; 2 km WSW, MVZ 150940–160299; 6 km WSW, 160300–333; 5 km SSW, 160334–49; 7 km SSW, 160350–51; 3 km NNW, 160353, 160360; 4 km NW, 163928–31, 163973; 2 km W, 171198–202; 4 km SW, 171220–41; 4 km N, 171242; 4 km W, 171173–97; 4 km NW, 171112–43; 5 km SW, 171215; 5 km S, 171203–14; 6 km W, 171163–72; 8 km W, 171144–62. Paquix-Todos Santos road, 4–7 km SE Todos Santos, MVZ 149198–206, 108616–30, 108631–72. 13.6 mi. (rd.) N Santa Eulalia along Rta. Nac. 9N, MVZ 149228. 5.1 mi. (rd.) N Santa Eulalia along Rta. Nac. 9N, MVZ 108673–95, 109296. Cumbre between Ixtiapoc and Villa Linda, el. 2,800–3,400 m, UMMZ 120007–08. Cumbre between Yaiquich and San Mateo Ixtatán, el. 3,000 m, UMMZ 120009. Todos Santos, el. 9,000–10,000 ft., UMMZ 120465–66, 120487. Mina Villa Linda, UMMZ 130073. 9 km (rd.) SW San Juan Ixcay, el. 2,900 m, UMMZ 120011. Rta. Nac. 9N, 7.4 mi. (rd.) SW San Juan Ixcay, MVZ 108696–728. Rta. Nac. 9N, 10.6 mi. (rd.) SW San Juan Ixcay, MVZ 108729–32. 8 km W San Mateo Ixtatán, el. 3,100 m, MVZ 171148–62. 3 km NNW San Mateo Ixtatán, el. 8,700 ft., MVZ 150940–1000, 160201–91, 160353, 160360; 4 km NW, 2,750 m, 171112–43. 2 km WSW San Mateo Ixtatán, el. 8,850 ft., MVZ 160292–

99; 2 km W, 2,750 m, 171198–202. 6 km WSW San Mateo Ixtatán, el. 9,150–9,450 ft., MVZ 160330–33, 160352, 160354; 6 km W, 171163–72. 5 km SSW San Mateo Ixtatán, el. 8,650–9,150 ft., MVZ 160343–49; 4 km SW, 2,835–2,965 m, 171220–41; 4 km W, 2,900 m, 171173–97; 5 km SW, 2,965–3,045 m, 171215–19; 5 km S, 3,150 m, 171203–14. 7 km SSW San Mateo Ixtatán, el. 9,650 ft., MVZ 160350–51. 4 km NW San Mateo Ixtatán, el. 2,750 m, MVZ 163928–31, 163973; 4 km N, 2,650 m, 171242.

CUILCO. Above Salquil Grande, el. 3,000 m, UMMZ 89116–18. 6.7 mi. (rd.) S Nebaj by Rta. Depto. 3, el. 2,500 m, MVZ 160992. On ridge 2.5 km W, 2 km (airline) N San Miguel Uspantán, el. 2,260–2,640 m, MVZ 149229–300.

Bolitoglossa rufescens. CUCHUMATANES. Vicinity Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 950–1,100 m, MVZ 134626–28.

Bolitoglossa rufescens. CUCHUMATANES. Vicinity Finca Chiblac, ca. 10 km (airline) NE Santa Cruz Barillas, el. 950–1,100 m, MVZ 134626–28.

Bolitoglossa stuarti (tentative identification). CUCHUMATANES. 15 km (airline) W La Democracia, el. 1,850 m, UMMZ 126781.

Bradytriton silus. CUCHUMATANES. Finca Chiblac, 15 km NE Barillas, el. 4,300 ft. (1,310 m), MVZ 131586, 131587 (holotype), 131589–94, 134635–37, 134638, 173063–64; LACM 134566.

Dendrotriton cuchumatanus. CUCHUMATANES. Along Rta. Nac. 9N, 8.5 km (rd.) SW San Juan Ixcay, el. 2,860 m, MVZ 113002 (holotype), 113003–05, 113007–19, 113021–22; LACM 105296–97.

Dendrotriton rabbi. CUCHUMATANES. Planes de Peña Blanca, 1.5 km (airline) NE Peña Blanca peak, el. 2,700 m, MVZ 105298–300, 149702–05, 149139. 2 km (airline) WSW San Mateo Ixtatán, el. 8,850 ft., MVZ 160437. 3 km (airline) NNW San Mateo Ixtatán, el. 2,750 m, 160422–36. Cloud forest above summit of road between El Reposo and Oja Blanca ca. 9 mi. by rd., SW El Reposo, el. 2,200–2,300 m, MVZ 109297–301.

CUILCO. 9.5 km W, 8.5 km S (airline), La Democracia, Montañas de Cuilco, el. 2,100–2,500 m, MVZ 114766–96, 143920–26, 103839 (holotype), 103840–78, LACM 105298–300. On ridge 2.5 km W, 2 km (airline) N, San Miguel Uspantán, el. 2,400 m, MVZ 160895–96.

Nyctanolis pernix. CUCHUMATANES. Finca Chiblac, 10 km (air) NE Barillas, el. 1,370 m (4,500 ft.), MVZ 131583–85, 134639–40, 134641 (holotype), 134642–44, 149370–73; MCZ 100154.

Pseudoeurycea rex. CUCHUMATANES. Vicinity El Retiro and Peña Blanca peak, el. 2,800–3,300 m, MVZ 149404–33, 149464–520, 149522–58, 149693–700. Vicinity Capzín, Rta. Nac. 9N, 50–60 km (rd.) N Huehuetenango, el. 2,900–3,300 m, MVZ 160973–82, 134211–401. 2–8 km N, W, and S (airline) San Mateo Ixtatán, el. 2,750–3,200 m; 5 km, MVZ 171243–52; 7 km SSW, 160410–19; 6 km WSW, 160409; 4 km NW, 167796–803. Between Cumbre Yaiquich and San Mateo Ixtatán, 3,000 m, UMMZ 120067. 10 km (rd.) SW San Juan Ixcay, el. 3,300 m, UMMZ 120068.

CUILCO. Above Salquil Grande, el. 3,000 m, UMMZ 89114–15.

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